

ECOLOGICAL AND EVOLUTIONARY EFFECTS OF INTERSPECIFIC COMPETITION IN TITS

ANDRÉ A. DHONDT¹

ABSTRACT.—In this review the evidence for the existence of interspecific competition between members of the genus *Parus* is organized according to the time scale involved. Competition on an ecological time scale is amenable to experimental manipulation, whereas the effects of competition on an evolutionary time scale are not. Therefore the existence of competition has to be inferred mainly from comparisons between populations. Numerical effects of interspecific competition in coexisting populations on population parameters have been shown in several studies of Great and Blue tits (*Parus major* and *P. caeruleus*) during the breeding season and during winter, and they have been suggested for the Black-capped Chickadee (*P. atricapillus*) and the Tufted Titmouse (*P. bicolor*). It is argued that the doubly asymmetric two-way interspecific competition between Great and Blue tits would have a stabilizing effect promoting their coexistence. Functional effects on niche use have been experimentally shown by removal or cage experiments between Willow (*P. montanus*) and Marsh (*P. palustris*) tits, between Willow and Crested tits (*P. cristatus*) and Coal Tits (*P. ater*) and Goldcrests (*Regulus regulus*), and between Coal and Willow tits. Non-manipulative studies suggest the existence of interspecific competition leading to rapid niche shifts between Crested and Willow tits and between Great and Willow tits. Evolutionary responses that can be explained as adaptations to variations in the importance of interspecific competition are numerous. An experiment failed to show that Blue Tit populations, subjected to different levels of interspecific competition by Great Tits, underwent divergent micro-evolutionary changes for body size. It thus remains unclear what time scale is involved in the presumed adaptations to interspecific competition.

The problem with interspecific competition is that some people believe it is such an important force which is a transient phenomenon that can be observed only rarely in nature, whereas others think it is so important that it permanently influences coexisting species-populations. This difference in opinion, also concerning titmice, existed 35 years ago. Kluyver (1951, 1966) wrote that interspecific competition between Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*) existed, but that since intraspecific competition among Great Tits was more important than interspecific competition between the two species, he would only consider the first. From the context of these statements it seems he meant that Blue Tit numbers influenced some aspect of Great Tit population dynamics. Unfortunately, he did not present evidence to support his claim.

Lack (1945) argued that closely related species coexisting in the same habitat differ in ecological niche, especially in foraging niche, in order to avoid competition. These niche differences are the result of their evolu-

¹ Dept. Biology, Univ. of Antwerp, U.I.A., B-2610 Wilrijk, Belgium.

tionary history, during which interspecific competition did occur. Forty years ago this was an important new idea, since it was then that the so-called Hypothesis of Gause, that closely related species must differ in their ecological niches in order to coexist, was being substantiated. Several of Lack's students (Hartley 1953, Gibb 1954, Betts 1955) provided data showing that, indeed, the five members of the genus *Parus* coexisting in Wytham Wood differed in their foraging niches. The large overlap in foraging niches in the breeding season was explained by stating that food was so superabundant then that no competition would take place. During winter, when food abundance was thought to be limiting, niches diverged, supporting the idea that birds avoided competition for food.

The most convincing, but not easiest, way to demonstrate the existence of interspecific competition is through field experiments. Schoener (1983) listed 164 experiments published before 1982. Only seven concerned birds, two of which were about titmice. Tits have, therefore, played an important role in the experimental study of interspecific competition in birds, a role they continue to play.

WHAT IS COMPETITION?

Competition is a biological interaction between individuals or populations (belonging to the same or to different species) for a limiting resource, resulting in a reduced fitness of all parties involved. Recently it has become fashionable to enlarge the definition and to include amensalism in the definition of competition, meaning that if only one of the parties involved is affected, this should also be called competition. Evidence for the existence of competition can either be provided by changes in population size (numerical response) or by a niche shift (Thomson 1980).

In the published literature, interspecific competition is accepted as having been demonstrated if an effect is shown on population size as such or on one of the population processes such as reproduction, survival, recruitment, immigration, or emigration (cf. Schoener 1983, Connell 1983). Competition can also influence the age structure of a population (Hairston 1980). The usual implicit assumption is that if there is an effect on one of the population processes, this will eventually influence population size also. Alternatively, if the age structure has changed, this must have been caused by a change in one of the population processes. I will therefore consider all such responses as belonging to the category of numerical responses. Thomson (1980) further subdivided niche shifts into two groups, nonevolutionary shifts of behavior which are functional responses to competition, and evolved shifts such as character displacements which are evolutionary responses.

Most students of interspecific competition are satisfied that competition is present if an effect can be demonstrated for one of the populations studied (amensalism). Very rare are the publications that provide evidence that both populations were affected. Another way to regroup the effects of interspecific competition is by considering the time scale which is involved. Numerical responses and "functional" responses occur rapidly on an ecological time scale, and they can thus be reversed immediately when conditions change. If competitive effects exist, they can be demonstrated by experimentation, and positive experiments would indicate that interspecific competition is a force that can be observed. Evolutionary responses operate over a longer time scale, and when conditions change, the populations respond more slowly. They are therefore not amenable to short-term experimentation. If demonstrated, they would support the idea that interspecific competition is an important evolutionary force shaping the composition of communities. One exception concerns competitive exclusion, which could be demonstrated experimentally through introductions of species absent from certain habitats or geographical ranges. I prefer to discuss the effects of interspecific competition according to the time scale over which they operate and will consider "ecological" effects and "evolutionary" effects. I realize that it is not always easy to separate between them, that given sufficient time one will lead to the other, and that several responses may occur together (Thomson 1980). Tit studies provide examples of all types of responses, although not all are equally convincing nor have they all been explained in the same way.

ECOLOGICAL EFFECTS OF INTERSPECIFIC COMPETITION

Numeric responses.—Although it is now considered that niche shifts are sufficient to conclude that interspecific competition does exist (see below) the older competition theory, based on equations such as the Lotka-Volterra equations, implied that numeric responses were needed before one could conclude as to the existence of competition. Very little literature showing such effects in birds, however, is available, perhaps because such data can be collected only over a much longer time period than data on niche shifts.

The Black-capped Chickadee and the Tufted Titmouse

One very interesting example is the study of the dynamics of a Black-capped Chickadee (*Parus atricapillus*) population for over 25 years by Loery and Nichols (1985). In the course of their study, the Tufted Titmouse (*Parus bicolor*) became established in their study site through natural expansion. They found that, following the establishment of the titmouse population, the chickadee population showed a short term (one

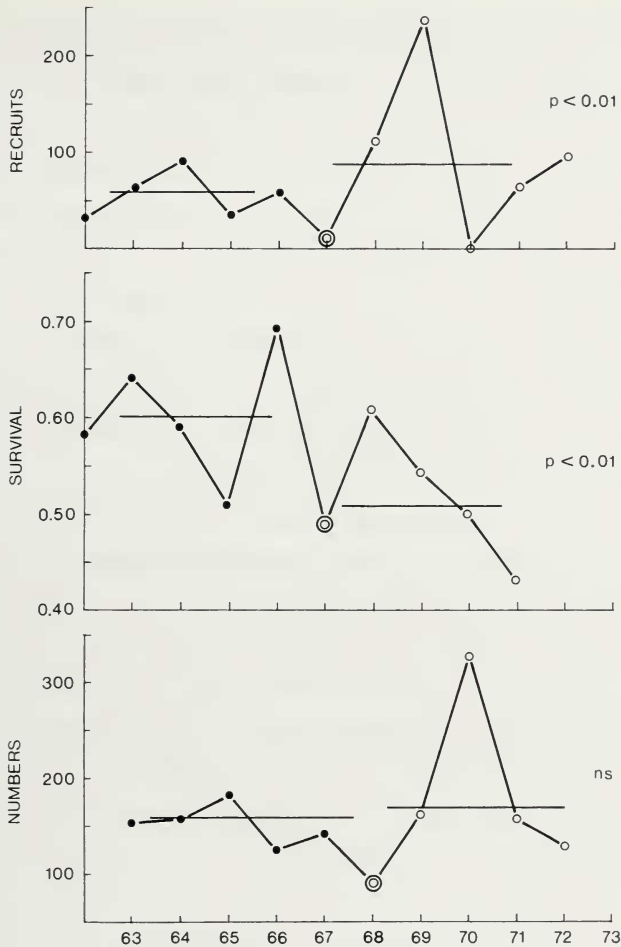


FIG. 1. Changes in population size (numbers), adult survival rate (survival) and numbers of immigrant birds (recruits) in a Black-capped Chickadee population before (filled symbols) and after (open symbols) the invasion by Tufted Titmice. The large circles indicate the value for the first year of the invasion. Horizontal lines represent average values for five-year periods before and after the invasion. Numbers and significance values as given by Loery and Nichols (1985).

year) but significant reduction in population size caused by a reduction of both the survival rate and the number of recruits (Fig. 1). They found, however, no long-term effect on population size, although when comparing the five-year periods before and after the establishment of the titmouse, a significant *decrease* in survival rate and a significant *increase* in number of recruits was found. As they pointed out (p. 1201), this

“natural experiment,” although highly suggestive for the existence of one-way interspecific competition between the Tufted Titmouse and the Black-capped Chickadee, is not conclusive. If we assume, for the sake of argument, that interspecific competition caused the changes in the population parameters of the Black-capped Chickadee, then we would conclude that the immediate numeric effect in the year following the establishment of the Tufted Titmouse was quite strong because both adult survival and recruitment of new birds was very low. The birds responded, however, very rapidly to the new situation whereby from the second year onwards, the number of recruits increased significantly but adult survival remained low. From the second year onwards after the settlement of the Tufted Titmouse, the increase in recruitment quantitatively compensated for the reduced survival, so that population size before and after the arrival of the titmouse were similar again, although the proportion of juveniles in the breeding population would have increased.

Great Tits and Blue Tits during the Breeding Season

The second example of interspecific competition between two tit species, the Great Tit and the Blue Tit, stems from my own work. The interesting aspect of this case is that, because these two species breed easily in nest-boxes, data are relatively easy to collect, and experimental manipulations have been carried out in the field. Furthermore, it is a rare case of a two-way doubly asymmetric interaction whereby during the breeding season the smaller Blue Tit is competitively superior (Dhondt 1977), and whereas during the non-breeding season the larger Great Tit has the upper hand (Dhondt and Eyckerman 1980a, b). Most probably this double asymmetry is a powerful stabilizing force which makes the coexistence of Great and Blue tits stable. This idea is supported by the analysis of *Parus* assemblages in European passerine bird communities by Herrera (1981). He found that in 78 out of 85 communities, in which at least two tit species were present, both Great and Blue tits were observed. In five communities, the Great Tit was present without the Blue Tit, and in one neither was present. In three communities, in which only one *Parus* species was present, neither Great nor Blue tits were found. These two species are thus both present in almost all situations throughout Europe in which tits are able to live.

During the breeding season, the Blue Tit has a negative effect on the reproduction of the larger Great Tit through exploitative competition for food. Both species feed mainly on the same species of caterpillars, but the Blue Tit eats the smaller instars, thus eating the food of the Great Tit before it becomes available for the larger species. Dhondt (1977) has shown for the Ghent study that significant negative correlations exist between Blue Tit breeding density and Great Tit reproductive rate (number of fledglings per pair and per season), mainly through an increased

nestling mortality in first broods and a reduction in the proportion of breeding pairs that start a second brood after having successfully raised a first brood. No reverse effect was found. Minot (1981) confirmed Dhondt's conclusions in part for the Oxford populations, showing that fledging weight, a good predictor of juvenile survival, was also inversely related to Blue Tit density. He also provided experimental evidence by manipulating Blue Tits. He removed all Blue Tit nestlings from one section of the woods and added them to another, keeping a third area as a control. He found that Great Tit young were significantly heavier in the area from which Blue Tits had been removed, compared to the two other areas, but he found no difference between the supplemented area and the control area. Török (1987) performed an interesting experiment in which he manipulated densities of Great and Blue tits in three plots, so that in the control plot both species could breed, and that in each of the experimental plots only Great or Blue tits bred. Over the three years of the experiment, he found no adverse effect of the Great Tit on the Blue Tit, confirming what Dhondt (1977) had found. He found no effect on the clutch size nor on the fledging success of the Great Tit and showed that Great Tit fledging weight was lower in the plot with Blue Tits compared to that without. This was, however, true only in two out of three years, which suggests that the importance of interspecific competition for food during the breeding season varies according to local conditions.

Additional effects of interspecific competition during the breeding season have also been found (Table 1). Thus Clobert et al. (1988) demonstrated non-experimentally that survival rate of male (only first year birds) but not of female Great Tits is negatively related to density of Blue Tits. Den Boer-Hazewinkel (1987) found that by experimentally removing Blue Tits before the start of the first brood, a higher proportion of the Great Tits will produce a second clutch, thus raising more young in a season. This suggests that some effects of competition operate over a longer time period. All these effects are probably the result of exploitative competition, although the result obtained by Clobert et al. (1988) is puzzling. They explained it as being caused by interference competition, whereby male Great Tits would have to expend more energy in territory defense, when Blue Tits are more numerous. My data from the Antwerp study showed that in the period 1979–1982, the adult survival rate of breeding Great Tits of both sexes differed between two experimental plots differing in Blue Tit but not in Great Tit density. Thus in Plot T (low Blue Tit density) adult survival was 54.5% ($N = 220$), but it was only 45.7% ($N = 278$) in Plot B (high Blue Tit density) (3-way G -test with Williams correction, effect sex: partial $G = 0.135$, 1 df NS; effect Plot: partial $G = 3.845$, 1 df, $P < 0.05$; Dhondt, unpubl. data).

No effects of Great Tit on Blue Tit reproduction have as yet been

TABLE 1
A SUMMARY OF THE EFFECTS OF BLUE TIT ON GREAT TIT DURING THE BREEDING SEASON

Source	Dhondt 1977	Minot 1981	Török 1987	Clobert et al. 1988	Dhondt, unpubl. data	Den Boer 1987
Site	Ghent	Oxford	Hungary	Oxford	Antwerp	Holland
Experiment	No	Yes	Yes	No	Yes	Yes
Clutch size	NS	0	NS	0	0	0
Fledglings/egg	+	0	+	0	0	0
Percent two broods	+	0	0	0	0	+
Fledglings/pair	+	0	NS	0	0	0
Fledgling mass	0	+	+ ^a	0	0	0
Adult survival	0	0	0	+ ^b	+ ^c	0

Notes: NS: no effect shown; +: significant effect; 0: effect not considered.

^a Effect detected in two years out of three.

^b Effect detected in yearling males only.

^c Effect detected in both sexes.

demonstrated when nest sites are superabundant, although Löhrl (1977) and Minot and Perrins (1986) have shown that the two species compete for nest sites if these are a limiting resource. This would be the result of interference competition, whereby the larger Great Tit would be more successful at securing nest sites than the smaller Blue Tit. Löhrl (1977) observed in several cases that when he hung a very low density of large-holed boxes in an optimal habitat, Blue Tits were killed by the Great Tits inside the nestboxes, emphasizing that interference competition could be rather vicious.

The data on interspecific competition between Great and Blue tits during the breeding season in six different studies, four of which are experimental, and in four different countries, all show that Blue Tits adversely influence one or more Great Tit population parameters (nestling survival, nestling weight, proportion of second broods, reproductive rate, adult survival). It can thus be concluded that there is strong evidence, both correlative and experimental, that during the breeding season Blue Tits adversely affect Great Tit reproductive output or effort. The exact parameter which is influenced, however, varied between studies, and competition could not be demonstrated in all years. Competition during the breeding season seems to be the result of exploitative competition for food.

Great Tits and Blue Tits outside the Breeding Season

Dhondt and Eyckerman (1980a, b) have shown experimentally that when Great Tits were excluded from the nestboxes in a plot by reducing

the size of their entrance hole to 26 mm, which made the boxes unsuitable for Great Tits but not for Blue Tits, the breeding density of the Blue Tit increased in the following breeding season by a factor of almost two and remained high for at least five years (Dhondt 1985). Although they showed that the number of Blue Tits roosting in nestboxes during winter increased when Great Tits had been excluded, their data were inadequate to determine what changes in population parameters caused this increase in Blue Tit density. A similar experiment by Löhrl (1977) gave a similar result, although he had no control area. He concluded, however, that the breeding density he observed (almost 4 pairs per ha) had never been found in any other study. That food could be involved in this winter competition was shown experimentally by Krebs (1971) who found that in a study plot in which food was added during winter, Blue Tit breeding numbers had increased in the next breeding season, whereas they had decreased in a control plot. Källander (1981), however, repeated a similar experiment in two different years and found that in one year Great Tit numbers increased in the plot with extra food, but he found no influence on Blue Tit population size. The importance of winter competition for food between Great Tits and Blue Tits therefore, seems to be limited. Intraspecific competition among Great Tits for food during winter also depends on the amount of natural food (beech mast) available and does not seem to influence all age classes in the same ways (van Balen 1980).

I started the Antwerp tit project in 1979, using the earlier conclusions to manipulate the level of interspecific competition. This allowed me to determine what differences, other than density, exist between Blue Tit populations in optimal habitat, exposed to or protected from Great Tit interspecific competition. The mechanism of winter competition is to a limited extent for food, but there certainly is greater competition for roosting sites. When nestboxes were made unsuitable for Great Tits, Blue Tits suddenly used them for roosting during winter in large numbers (Dhondt and Eyckerman 1980a, Dhondt, unpubl. data).

Dhondt et al. (1982) have shown that in a high density area, Blue Tit territories covered the entire plot, whereas in the low density plot open space remained between the territories. In such low density areas, therefore, Blue Tits seem to be winter limited (through interspecific competition), whereas in the high density areas they seem to be summer limited (through intraspecific competition). Although the complete analysis of the results has not yet been performed, I will present some conclusions that are already clear. These are based on the comparison of two study plots, about 600 m apart, both of about 12 ha (B and T) in the Peerdsbos, a wooded estate of ca 150 ha near Antwerp. In both plots, nestboxes were superabundant. In Plot B the nestbox configuration remained unchanged

throughout the study period, with 118 large-holed and 59 small-holed nestboxes which provided Blue Tits with a refuge from the winter competition by Great Tits. This resulted in Great and Blue tit populations at high densities. In Plot T 80, 120 large-holed nestboxes were available later in the breeding seasons of 1979–1983, and 120 small-holed nestboxes since then. In Plot T, during the first five years, Great Tit densities were high, and Blue Tit densities low compared to Plot B (1.83 pairs per ha, and 2.42 in Plot B). In the following four years, Great Tit density was very low, and Blue Tit density high (2.75 per ha compared to 2.46 in Plot B). The breeding densities of Blue Tits were thus as expected from the experimental results obtained by Dhondt and Eyckerman (1980a) at Ghent and reflected the expected effects of interspecific competition. Nearly all breeding birds were trapped on the nest, so that complete data were available on reproduction, local recruitment (recruitment of locally born breeding birds into the breeding population), immigration (recruitment of non-local birds into the breeding population), and adult survival.

This experiment provides information on the effect on interspecific competition of Great Tits on Blue Tit population parameters. Plot B is kept as a control. Plot T was changed from a low density, high interspecific competition situation (first period) to a high density, low interspecific competition situation (second period). The main findings are that (Dhondt, unpubl. data): (1) there is no clear difference in reproductive rate (number of fledglings per pair and per season) between the plots, nor between the periods in Plot T; and (2) there is a difference in adult survival rate. For both sexes combined the survival in Plot B was 35.6% ($N = 191$) in period 1 (1979–1982) and 27.6% ($N = 225$) in period 2 (1983–1986). This decrease in survival, that was also observed for Great Tits and in a third Blue Tit area, was probably caused by three severe winters. In Plot T, however, the survival increased from 34.5% ($N = 139$) in period 1 to 37.6% ($N = 223$) in period 2. During period 1 the survival rate did not differ between the plots ($G = 0.040$, 1 df, NS), but during period 2, survival was significantly higher in Plot T ($G = 5.207$, 1 df, $P < 0.05$). This suggests that through the experimental reduction of the interspecific competition by Great Tits in the second period in Plot T, adult survival of the Blue Tits increased, although Blue Tit density had also increased. (3) In males, but not in females, the proportion of local recruits in the breeding population increased in Plot T in the second 4-year period (1984–87) compared to the first 4-year period (1980–1983), although it decreased in Plot B. A two-way ANOVA on the proportion of local recruits (angular transformation), with plot and period as the factors, yields a significant plot \times period interaction ($F = 14.106$, 1, 15 df, $P < 0.01$), showing that through the change in the experimental setup in Plot T, local born males made

up a larger proportion of the breeding recruits. (4) In males, but not in females, the proportion of immigrant recruits decreased in Plot T but increased in Plot B. A two-way ANOVA again shows that a significant interaction plot \times period existed ($F = 11.177$, $df = 1,15$, $P < 0.01$). Immigrant males thus formed a smaller proportion of the breeding population in Plot T during the second period when breeding density had increased through a reduction of the interspecific competition, whereas this was not the case in Plot B.

The effect of Great Tit interspecific competition on Blue Tit population parameters thus operates mainly on the juvenile males, since fewer juveniles recruit locally in the low density situation with interspecific competition, and a larger proportion of the breeding population has therefore emigrated. Adult survival of both sexes also seems to be higher in the high density situation. A low density Blue Tit population suffering from interspecific competition by the Great Tit, therefore, has a larger genetic turnover compared to a high density population protected from the Great Tit.

It is interesting to underline that, in essence, this is the same result as the one obtained by Loery and Nichols (1985), who found that the Black-capped Chickadee population had a lowered adult survival, but an increased immigration after the Tufted Titmouse arrived. In their case, these changes compensated one another, so that local population size remained unchanged. In the Blue Tit, changes in the population parameters did not compensate one another, so that an increase in the breeding population was observed.

The Foraging Niche of Tits in the Presence and Absence of Congeners

Changes in foraging niche have been used extensively to provide evidence that interspecific competition exists and were recently reviewed by Alatalo (1982) and Alatalo et al. (1986). In the context of the reasoning developed in this paper, I want to differentiate between "functional" and "evolutionary" responses.

Examples of functional responses are relatively few. If they exist, they must be found in single study plots in which on different territories the flock composition differs. The advantage of studying tits is that many species defend group territories in winter and that the group territories of many species overlap to a large extent. The differences in flock composition may be natural or experimental.

A first example is provided by Alatalo (1981). He observed that in mixed-species winter flocks in one study area in northern Finland there was a clear niche shift of the Willow Tit (*P. montanus*) in relation to the

presence/absence of individuals of a more dominant species (Crested Tit [*P. cristatus*]), in which the Willow Tit shifted away from the species of trees occupied by the Crested Tit in flocks in which it was present, as compared to neighboring flocks in which it was absent. Similarly, Willow Tits shifted away from the parts of the trees occupied by the Great Tit or by the Crested Tit when these were present in the same flocks. Alatalo et al. (1985, 1987) experimentally confirmed the existence of interspecific competition for foraging sites in winter. In an area in which Willow, Crested, and Coal tits (*Parus ater*), and Goldcrest (*Regulus regulus*) spent the winter together in mixed-species flocks of constant composition, they reduced the number of Willow and Crested tits which mostly use the inner parts of the trees (Alatalo et al. 1985) and reduced the smaller species which mainly feed on the outer parts of the tree in a second experiment (Alatalo et al. 1987). In both experiments, they observed an increase in the use of the tree parts vacated by the removed species. Thus, the smaller Coal Tit and Goldcrest increased their foraging in the inner canopy when the larger Crested and Willow tits had been removed. They repeated this experiment in three experimental plots, having at the same time observations from three control plots. This convincingly showed that interspecific competition existed against the smaller species. The reverse experiment, i.e., the removal of the smaller species resulted in an expansion of the foraging of the larger species at the end of winter towards the outer parts of the tree. This was true for both Willow and Crested tits in pine trees but for the Crested Tit only in spruce trees. Alatalo et al. (1985) have thus shown that in winter there is two-way interspecific competition between Crested and Willow tits on the one hand and between Coal Tits and Goldcrests on the other. Exploitative competition was certainly involved in the niche shift of the larger species. In the smaller species, it could have been interference competition, exploitative competition, or both. In a cage experiment, Alatalo et al. (1986) showed that the smaller Coal Tits used the outer parts of the tree in the presence of Willow Tits but used inner parts in their absence. Willow Tit tree use did not differ in relation to the presence or absence of Coal Tits. It should be emphasized that in these examples no experimental evidence is given for competition between Willow and Crested tits (but see below).

A second example stems from observation in Belgium. It demonstrated that at high wind velocities tits shift their foraging sites. Such a niche shift also happens in relation to temperature (Grubb 1978), but the interesting feature of the wind effect is that strong winds are usually of short duration, so observations on different days are, on the whole, independent of one another because they are separated by days with normal wind. The studies of Ysenbaardt (1987) and Lens (1988) on Crested and Willow tits

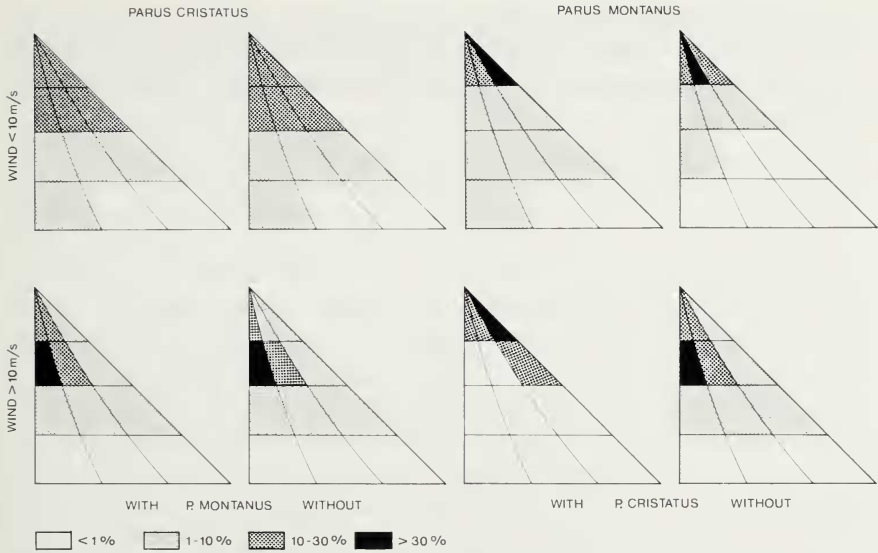


FIG. 2. Foraging niches of Crested and Willow tits in a pine forest in N. Belgium. Above: low wind speed; below: high wind speed (> 10 m/s). From left to right: foraging niche of Crested Tits on territories with Willow Tits; of Crested Tits with no Willow Tits; of Willow Tits with Crested Tits; of Willow Tits with no Crested Tits. Note that at high wind speeds Crested Tits always move to lower and more inner parts of the tree, but that Willow Tits only do that in the absence of Crested Tits. Willow Tits move to outer and higher parts of the tree on days with high wind speeds. (From Ysenbaardt 1987 and Lens 1988).

in a pine forest in northern Belgium showed that on days of low wind velocity, the foraging niches of the two species were not affected by the presence of the second one. However, on days of high wind velocity (> 10 m/sec) Willow Tits in territories without Crested Tits significantly shifted their foraging sites to lower and more inner parts of the trees. Crested Tits also shifted their foraging sites to a lesser extent, towards lower and more inner parts of the tree; but Willow Tits on territories with Crested Tits moved up and out. Lens (1988) simultaneously observed an increase in the number of chases of Willow Tits by Crested Tits, suggesting that interspecific intolerance was the direct cause of the displacement of Willow Tits from more preferred parts of the tree, but only under conditions of environmental stress.

These examples show that, in coniferous habitats at least, interspecific competition between tits exists in ecological time. Although the observed changes in niche use were not related to changes in survival, it is probable they would have such an effect, since two experimental studies have shown that overwinter survival increased when additional food was offered dur-

ing winter. This shows that small tits in climatically extreme environments are food limited during winter (Willow and Crested tits in Sweden: Jansson et al. 1981; Black-capped Chickadee in Wisconsin: Brittingham and Temple 1988).

Evolutionary Effects of Interspecific Competition

Evolutionary effects cannot normally be experimentally demonstrated because of the time scale involved. Evidence, therefore, must be circumstantial, but if this evidence shows a pattern that is as predicted from the ecological effects of competition, it can become very convincing. In some of the examples below it is unclear what is the exact time scale involved. I have included them in this section because no experimental evidence is available yet which shows that interspecific competition does actually occur between the species discussed. Four categories of evidence are normally used: (1) Allopatric distribution of sibling species, (2) Habitat segregation and non-random assemblage of congeners in communities, (3) Niche segregation in sympatry and divergence of niches in sympatry compared to allopatry, and (4) Character displacement. Many of these arguments are discussed in detail by Lack (1971), and I will refer only to arguments published since then. Lack concluded (p. 36): "The European tits were selected for ecological study because of their apparent complexity, and in particular because several species usually coexist in the same habitat. Nevertheless, each species is segregated from every other, in a few cases by geographical range, in many by habitat, and in yet more by a difference in food and feeding stations in the same habitat. Differences of this last type are associated with adaptive differences in overall size and in size of beak, the larger species tending to feed lower down, and on larger insects and harder seeds, than the smaller species. Likewise the species which live in coniferous forest have longer and narrower beaks than those in broad-leaved woods. Some species have a different, or unusually wide, habitat in a small part of their range, often linked with the absence of another species, and the beak may be appropriately modified." Lack believed that segregation by range or by habitat is the result of competitive exclusion. This exclusion need not be because of competition with congeners alone, but it can also be the result of competition with a group of other passerines. A nice example of interspecific competition for space between the Great Tit and the Chaffinch (*Fringilla coelebs*) on a small island off the coast of Scotland was recently described by Reed (1982).

Community Composition of Tits in Europe

Herrera (1981) analyzed 88 European passerine bird communities in which at least one species of *Parus* was present. He found that only about

one third of all possible combinations with the six available species were observed, whereby mean interspecific difference in bill length was significantly higher in the combinations which were observed. He concluded that the *Parus* assemblages were the result of competitive interactions for "some sort of complex combination of prey size, prey type and micro-habitat," whereby species absent from assemblages were excluded through interspecific competition.

The Foraging Niche of Tits in Sympatry and in Allopatry

Sympatric species of tits often use different habitats and are thus, in Lack's terminology, ecologically segregated by habitat. Among European tits, 32% are isolated by habitat (Lack 1971, p. 59). Habitat use differs, however, over the geographic range of the species. Thus, for example, Blondel (1985) has shown that the three tit species that breed on the island of Corsica strongly broadened their habitat niche compared to those on the mainland. Other examples concern the Willow Tit, that is limited to coniferous habitats in Scandinavia, but is a regular breeder in deciduous habitat in Western Europe, and of the Crested Tit that occasionally uses broad-leaved habitat in western and southern Europe but never in Scandinavia. Such species are ecologically segregated from congeners by habitat in part of their range but by feeding niche in others (cf. Lack 1971, p. 261). These observations give no solution to the problem of whether competition exists today, or whether the actual situation is the result of adaptation to local situations under the influence of competition in the past. However, Alatalo and Lundberg (1983) concluded, as a result of aviary experiments in which Marsh (*Parus palustris*) and Willow tits were given a choice to forage on oak or spruce branches, that in Scandinavia, Willow Tits would be competitively excluded from deciduous habitat by the presence of Marsh Tits.

The foraging niches of tits, especially during winter, are very well studied. Essentially all authors find that the average foraging niche differs between coexisting species but that there is a considerable amount of overlap. Lack calculated that 43% of the European tits are ecologically segregated by feeding station (Lack 1971, p. 59). The interpretation of such non-experimental data can be that these differences are the result of interspecific competition in the past, and permits coexistence with no significant competition (Gibb 1954, Lack 1971) or that they still lead to interspecific competition for food in the present day. This latter point of view is the more popular today, and evidence for it has recently been reviewed by Alatalo (1982) and by Alatalo et al. (1986). The argument is that when one compares the foraging niche of a species in sympatry and in allopatry with a second species, a divergent niche shift in sympatry is suggestive of the existence of interspecific competition in sympatry. Ala-

talo et al. (1986) accept that "differences in the biotic or abiotic environment, irrespective of the presence or absence of putative competitors, may produce changes in foraging sites. The question is whether environmental causes can create *general* tendencies toward divergent rather than convergent changes." Alatalo et al. (1986) found such a general tendency towards divergence in sympatry and therefore concluded that non-experimental data demonstrate that interspecific competition does exist between sympatric tits. The problem with this kind of evidence is that, although it will convince the convinced, researchers who do not believe that interspecific competition is continuously important on an ecological time scale, might argue that the differences one finds when comparing sympatric and allopatric foraging niches could be the result of an evolutionary response rather than of an ecological response as defined above, and simply confirm Lack's thesis.

In conclusion then, during winter some species of sympatric tits living together in the same habitat compete interspecifically for preferred foraging sites. This conclusion is supported by all categories of arguments summed up above, i.e., segregation by range, by habitat or by feeding station, which can all be interpreted as having come about because of interspecific competition. This implies that the composition of passerine communities would be affected, to an important degree, by interspecific competition. These arguments by themselves do not tell us how often this competition takes place.

Character Displacement

The final part of this review addresses evolutionary changes in tit population which could be explained through effects of interspecific competition. Lack (1971) summed up the examples of character displacement known in tits, in which the clearest example was that of the Blue Tit in the Canary Islands (Lack and Southern 1949). Two more recent examples have also been found.

Herrera (1978) described a situation in southern Spain in which he studied tits in two neighboring evergreen broad-leaved oak woodlands 175 km apart. In one locality he found only Great and Blue tits and in the other also the Crested Tit, although the passerine communities of the two areas were otherwise identical. He found a clear example of a character shift in the bill lengths mostly of Blue Tits. In zones of sympatry, the bill length of Blue Tit and Crested Tit differed by 0.75 mm, whereas in allopatry the difference was only 0.1 mm. Great Tits showed no differences in bill length between the two populations. These changes in morphology coincided with niche shift in foraging sites, in which the Blue Tit food niche was more compressed in the three-species locality. Surprisingly, the numeric response was not as expected, since in the two-species locality

Blue Tits were relatively more abundant and Great Tits relatively less abundant than in the three-species locality.

A second example concerns the Coal Tit on the Swedish island Gotland (Alatalo et al. 1986). There, Coal Tits are larger than on the mainland, in the absence of demonstrated competitors, since both the larger Crested and Willow tits are absent on Gotland. Again, the change in morphology coincides with a shift in foraging niche, in which the larger Coal Tits of Gotland forage more on the inner parts of the trees, while on the mainland they feed mostly on the outside of the tree and on needles.

Both examples show that when tit communities differed, this coincided with a change in morphology in allopatry so that the smaller species was larger. The most likely explanation of these observations is that through the absence of competitors of different species, there was a selective pressure for the smaller species to become larger. In Spain, the larger species (the Great Tit) did not change in morphology. In Gotland, the effect of increased intraspecific competition was illustrated very nicely, with the larger males showing the strongest change in foraging niche. A question that has not been answered yet is, how rapidly does such a change occur or, in other words, can such a morphological change in relation to interspecific competition be experimentally induced?

In order to answer this question consider my Antwerp studies of Blue Tits, experimentally subjected to different levels of interspecific competition by Great Tits. When I began investigations in 1979, I knew that body size was heritable, at least in Great Tits (Garnett 1976), and that environmental changes could result in micro-evolutionary changes in Great Tit body size (Dhondt et al. 1979). I confirmed experimentally that Blue Tit tarsus length was heritable in my populations (Dhondt 1982, 1988). If interspecific competition were a powerful selective force on body size, I expected a rapid divergent micro-evolutionary change in body size between populations subjected to different levels of interspecific competition. I therefore studied the between-year variations in tarsus length of Blue Tits in three populations subjected to different levels of intra- and interspecific competition. My study started after an extremely cold winter (1978–79), and during the course of the study, four other cold winters were observed. I did observe relatively large between-year variations in nestling tarsus length that, however, were parallel in the three plots, but I found no differences between the plots (Dhondt 1988). These differences were the result of differences in body size of the recruits into the breeding population in relation to winter cold; after cold winters, both male and female recruits were larger, and since recruits made up between 50 and 70% of the breeding population, the body size of nestlings was larger after cold winters (Dhondt, unpubl. data). Since no differences could be demonstrated between plots, interspecific competition could not be shown to

have had an effect on the body size of the birds. In this situation of non-isolated populations subjected to different levels of interspecific competition, it did not cause divergent micro-evolution between the plots.

In conclusion, I think there is a considerable body of evidence that among tits interspecific competition exists in ecological time. A population suffering from interspecific competition shows a larger population turnover caused by a reduction in adult survival, a reduction in juvenile local recruitment, and an increase in recruitment through immigration. The effect may influence only one sex (males) or age-class (juveniles). If population size is limited through intraspecific competition during the breeding season, this will not cause an increase in the size of the breeding population but only a change in the age composition. In one of the two examples a decrease in population size in the population with interspecific competition was observed, in the other, this was not observed. This suggests that interspecific competition acts via a reduction in apparent habitat quality to the species suffering from this interaction. If, as is the case for Blue Tit and Great Tit, the interspecific competition influences both species but in an asymmetric way and in different seasons. This competition seems to have a stabilizing effect that promotes coexistence. In order to stand, however, this conclusion will have to be tested in appropriate models (P. Chesson pers. commun.).

Interspecific competition also leads to a narrowing of the niche space available, mainly in the winter season when food is probably limiting. Some experimental evidence proves this for a small number of European tits living in conifers. Much circumstantial evidence suggests that this is generally true. The effect of interspecific competition during only one season, in which the larger species usually are dominant, may have a destabilizing effect, which can lead to competitive exclusion of the subordinate species. In Scandinavia, some habitats contain only one species of tit (Hogstad 1978). Recent experiments in Norway (Steinar Helle, in litt.) suggest that on small islands, Willow and Crested tits competitively exclude one another. Willow Tits introduced on islands of the west coast of Norway, on which only Crested Tits lived, nearly all disappeared. Two that remained did not breed. The size of the Crested Tit population was not affected.

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